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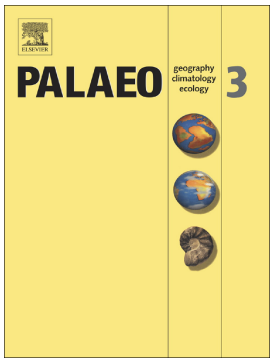

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Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela

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Abstract

Coprolites (fossil feces) provide important paleoecological information, such as diet of the producer, parasite infestation and gut microbiota, which cannot be accessed through body remains. The Late Miocene Urumaco Formation, in western Venezuela, has a diverse vertebrate fauna composed of ground sloths, rodents, reptiles, fishes and amphibians, as well as coprolites. Here we describe 106 coprolites produced by a range of carnivorous and herbivorous vertebrates, classified into five different morphotypes based on their size and shape, suggesting different producers. Herbivorous morphotypes (M1, M2 and M5) are the most abundant (59%). The most common inclusions in these coprolites are Poacea remains, although Eudicotyledoneae fragments, bacteria and cyanobacteria filaments were also found. The M1 morphotype is a bullet shape with longitudinal grooves; the M2 morphotype is round to oval, with at least one distinctive tapered end; and the M5 morphotype is a short cylinder with a rough surface, and rounded ends. In contrast, the morphotypes M3 and M4 are attributed by us to carnivores and have different inclusions. While M3 is a large cylinder with rounded ends and contains bacteria, nematode eggs and phytoliths, M4 is sausage-shaped and has muscle cells preserved inside. Based on the co-occurring fauna and the morphology of the coprolites, the probable producers were inferred as the following: M1, a rodent; M2, a notoungulate; M3, a crocodilian; M4, an indeterminate carnivore; and M5, a sirenian. The preservation of herbivorous and carnivorous coprolites with bacterial, parasitological and muscle remains in the same formation and even the same outcrop is rare in the geological record. This unique association and preservation suggests early lithification promoted by rapid burial, although the presence of the boring trace *Gastrochaenolites* in a single specimen indicates some degree of time-averaging.

Key-words: Fossil dungs, estuarine/coastal environment, *Gastrochaenolites*, Neogene, South America.

1. Introduction

Since the early 19th century, when coprolites were first described by Buckland (1829), the paleoecological significance of fossil feces has been made evident. Nevertheless, throughout the intervening 150 years, coprolites have remained poorly studied. In the last few decades, however, coprolites started to

attract paleontological attention due to the unique microenvironment formed inside them that enhances the fossilization potential of soft tissues, while also preserving paleoecological interactions that would otherwise go unrecognized (e.g. Qvarnström et al., 2016). Evidence of ecological phenomena, such as interactions between secondary and primary consumers (e.g. Chin et al., 2003; Eriksson et al., 2011; Nakajima and Izumi, 2014; Zatoń and Rakociński, 2014; Zatoń et al., 2015; O'goghain et al., 2016), herbivory (e.g. Scott, 1977, Chin, 2007; Hagström and Mehlqvist, 2012, Bajdek et al., 2014), detritivory (Falcon-Lang et al., 2015), parasitism (e.g. Fugassa et al., 2006; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013; Wood et al., 2013; Da Silva et al., 2014; Hugot et al., 2014; Zatoń and Rakociński, 2014; Bajdek et al., 2015) and symbiosis (e.g. Chin, 2007; Santiago-Rodriguez et al., 2013; Badjek et al., 2015; Dentzien-Dias et al., 2017) has led ichnologists to consider coprolites as Konservat-Lagerstätten (Seilacher et al. 2001; Qvarnström et al, 2016).

However, the majority of vertebrate coprolites in the fossil record were produced by carnivores rather than herbivores (see, for example, Chin, 2002; Chin et al. 2003, Northwood, 2005; Chin, 2007; Dentzien-Dias et al., 2012; Bajdek et al., 2015; Niedźwiedzki et al., 2016; Bravo-Cuevas et al., 2017). This might happen because herbivorous feces are composed of a large quantity of undigested food attracting a wide variety of scavengers (Chin et al., 2009) and/or because the dietary composition influenced their preservation. The carnivore feces are poor in nutrients (attracting fewer scavengers), being decomposed mainly by microbials, and the calcium phosphate derived from bone digestion acts as a permineralizing agent (Hunt et al., 1994; Chin, 2002;

Hollocher and Hollocher, 2012; Dentzien-Dias et al., 2017; Rodrigues et al., 2018), facilitating the preservation.

In some cases, the morphology of the coprolite can indicate the producer, as, for example, spiral coprolites are often attributed to non-teleost fishes (Williams, 1972; Jain, 1983; McAllister, 1985; Souto, 2008; Dentzien-Dias et al., 2012; Niedźwiedzki et al., 2016). However, feces from different groups of animals can be similar in appearance, and variations can occur within the morphology of feces among a single producer, mainly due to different food and water availability and diseases (McAllister, 1985; Thulborn, 1991; Chin, 2002, 2007, 2008; Chame, 2003; Bisceglia *et al.*, 2007; Colares *et al.*, 2010; Milàn, 2012; Lucas et al., 2012). Although, in some cases, the morphology is not enough to determine the animal source (Francischini et al., 2017), coprolite shape, together with inclusions, makes it possible to determine the producer.

Different interactions of vertebrates and invertebrates can be preserved in coprolites, such as surface traces, which are a clear evidence of coprophagy. Coprophagy can be indicated by biting traces, scratches or burrows on the surface of the coprolite or even in its interior (Chin and Gill, 1996; Wahl et al., 1998; Godfrey and Smith, 2010; Milàn et al., 2012; Godfrey and Palmer, 2015).

In this paper, we describe vertebrate coprolite assemblages from the Upper Miocene Urumaco Formation (Venezuela), which were collected from five vertebrate-bearing localities (El Vijiadero (Sur Llano Grande), Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio). We described different coprolite morphotypes, composition and inclusions, as well as associated traces.

2. Geology

The Urumaco stratigraphic sequence is composed of seven geological units (Quiroz and Jaramillo, 2010), represented by diverse paleoenvironment facies including marine, estuarine, riverine, lacustrine and terrestrial (Díaz de Gamero and Linares, 1989; Quiroz and Jaramillo, 2010; Carrillo-Briceño et al., 2015). Throughout the entire section (Quiroz and Jaramillo, 2010), the lithology varies between more terrestrially influenced beds such as coal seams, and marine-influenced facies including sandstones, limestones and shales, and the associated marine, estuarine, and freshwater fauna (Table 1 and 2; e.g. Sánchez-Villagra and Aguilera, 2006; Sánchez-Villagra et al., 2010; Aguilera et al., 2013; Scheyer et al., 2013; Carrillo-Briceño et al., 2015; Aguirre-Fernández et al., 2017) provide unequivocal evidence of a marine coastal/estuarine environment.

The Urumaco Formation (Upper Miocene) has a thickness of approximately 1700–2060 m, and the lower and upper contacts (Fig. 1) are conformable with the Socorro and Codore formations, respectively (Quiroz and Jaramillo, 2010). The unit is divided informally in to three members: the Lower Member (615 m thick), Middle Member (755 m thick) and Upper Member (330 m thick), and the unit is interpreted to represent a variety of marine/continental environments of a prograding strandplain-deltaic complex (Quiroz and Jaramillo, 2010). Among the studied localities, El Vijiadero (Sur Llano Grande) and Quebrada Bejucal belong to the Lower Member, and El Mamón, Corralito

and Tío Gregorio to the Upper Member (Table 1). The lithology and paleoenviroments of these Urumaco Formation localities are shown in Table 1.

The El Mamón, Corralito and Tío Gregorio localities were deposited in an estuarine/coastal lagoon, delta plain and floodplain environment, while Quebrada Bejucal was deposited during a transgression in an interdistributary bay and El Vijiadero (Sur Llano Grande) was formed in a floodplain.

3. Material and Methods

The coprolites from the Urumaco Formation described here consist of 106 specimens, and come from five localities (Fig. 1, Tables 1–2, Supp. tab. 1). Coprolites were collected *in situ* (Fig. 2) by the authors (JDCB and RS) during several expeditions beginning in 2007.

The coprolites were described and classified in five morphotypes according to their morphology, size, surface features and types of inclusion, probably reflecting different producers. Measurements of the coprolites were taken with the aid of a digital vernier caliper. Surface features (plant impressions, borings, folds and bite traces) and adhesion structures were observed and noted in the data base. Plant fragments present on the coprolite surface were identified based on size and organization of venation (Esau, 1965; Mauseth, 1988; Evert, 2006) and, posteriorly, counted in order to estimate the proportion between Poacea and Eudicotyledoneae. The former family is characterized by leaves with parallel venation and bundles formed by cells of uniform size. In contrast, most of the eudicotyledonean leaf venation is

composed of anastomosed, branching and netted bundles, with cells of varying sizes (Esau, 1965; Mauseth, 1988; Evert, 2006).

The studied material is housed in the Alcaldía Bolivariana de Urumaco (AMU-CURS), Venezuela, and in the Laboratório de Geologia e Paleontologia (LGP) of the Universidade Federal do Rio Grande (FURG), Brazil (Supp. Tab. 1).

Eight coprolites, of different morphotypes (from the Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio localities), were transversely sectioned to expose the central portion. This portion was mounted on Al stubs, coated with Au and subjected to analysis under a JEOL JSN–6610LV Scanning Electron Microscope (SEM) at the Centro de Microscopia Eletrônica (CEME-Sul) of the FURG. Energy-dispersive X-ray spectroscopy (EDS) analyses were also conducted in six coprolites (Morphotypes M1, M2, three M3 and M4) to determine the chemical composition of the fecal matrix. Sample preparation followed standard procedures outlined by Mahaney (2002).

Another four specimens of M1, M2 and M3 (two coprolites) morphotypes and localities (Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio) were sectioned to produce thin sections, for the recognition of inclusions and petrographic fabrics. In one M3 coprolite, from the Quebrada Bejucal locality, longitudinal and transverse sections were made. The slides were analyzed with a Leitz Aristomet® photomicroscope with normal and polarized light at the LGP-FURG.

Microbial content was classified according to Northwood (2005), Hollocher and Hollocher (2012) and Bajdek et al., (2016) among others.

4. Results

Coprolites (106 specimens) were collected in five different localities of the western area of the Falcón State, Venezuela. These coprolites have different morphologies (described below) and sizes, ranging from 17 to 200 mm in length and 12 to 85 mm in width (Table 3), and five morphotypes were identified (Fig. 3). However, some coprolites could not be classified due to their very fragmented and/or weathered condition. Their color varies from yellowish to dark brown (Hue 10YR and Hue 2.5Y) and all morphotypes have sand adhering to their surfaces.

All the EDS analyzed coprolites (LGP-H566, LGP-H567, LGP-H571 and LGP-H572) belonging to the morphotypes M1, M2, M3 and M4 revealed similar compositions of Oxygen, Calcium and Phosphorus, suggesting a composition of calcium phosphate (Supp. Fig. 1–4; Supp. Tab. 2). The phosphatic mineral matrix is well known to promote rapid coprolite fossilization (Hunt et al., 1994; Chin, 2002; Hollocher and Hollocher, 2012). Additionally, some M3 coprolites present well formed rhombohedral crystals of calcite inside gas vesicles (Supp. Fig. 5).

4.1. Description of the coprolites

4.1.1. Morphotype M1

This morphotype comprises usually small (ranging in length from 17 to 41 mm and width 12 to 38 mm) coprolites with a bullet-shape (Fig. 4; Table 2).

These coprolites are anisopolar, one of the poles being flattened or concave, and the other rounded or tapered. The external surface bears parallel longitudinal striations or grooves impressed in the fine-grained matrix, radiating from the tapered pole and covering more than two thirds of the entire coprolite (Fig. 4A–C). These striae can occur along all the coprolites and are regularly spaced (approximately 1 mm). Usually the M1 morphotype occurs as isolated pellets; however, in few specimens (LGP-H566), it occurs in clusters of up to six coprolites, clearly produced during a single defecation event. This morphology is known since the Permian and is named *Alococoprus triassicus* (Hunt et al., 2007). Poacea and Eudicotyledoneae remains were found inside the M1 coprolites (Fig. 4D–E), Poacea being the more common inclusions (about 90% of total organic remains). In addition, possible trilete pollen (Fig. 4F) was also found. In the SEM analyses, some oval structures were found with 0.96 to 1.19 µm length and 0.74 to 0.75 µm widths (Fig. 4G). The size and shape of these structures lead us to interpret them as being bacterial in origin.

4.1.2. Morphotype M2

Rounded to oval coprolites, with at least one distinctive tapered pole, range in length from 23 to 52 mm and in width from 18 to 31 mm. Some materials have a folded area at their anterior portion (i.e. the first part to be evacuated) (Fig. 5B). The M2 coprolites are composed of a slightly coarse-grained matrix and are rich in plant remains, which vary greatly in size and are up to 18 mm in length (Fig. 5C–F and I–J).

In the thin sections and SEM analyses it is possible to see the organization of the plant tissues included in the M2 coprolites. These vegetal remains have square-shaped to rounded cell walls in cross-section and are arranged in parallel rows (Fig. 5E–F, I). Longitudinal striations allow the identification of a possible plant cuticle (Fig. 5E). These characteristics are typical of Poacea, and represent 80% of the plant fragments in the M2 coprolites. Stomata were observed in the plant fragments analyzed under the SEM. (Fig. 5J).

Two colonies of simple and filamentous cyanobacteria organized in trichomes (strands of vegetative cells) were identified in a thin section of an M2 coprolite (Fig. 5G–H). No evidence of a gelatinous sheath around the filament was found, only the trichome. The better preserved individual cells are rectangular (shorter than large) and form a filament composed of 19 individual cells, with approximately 100 µm length and 10 µm in diameter (Fig. 5H). The trichomes are similar to those of the order Oscillatoriales, family Oscillatoriaceae (Komárek and Hauer, 2013). This order of cyanobacteria was already recorded in Triassic coprolites of Australia (Northwood, 2005).

The second filamentous cyanobacteria colony is composed of trichomes with rounded to oval cells (Fig. 5G). The filament is approximately 75 µm long and has six individual cells, with diameter of 16 µm. These trichomes are similar in size and shape to those of the order Nostocales (Komárek and Hauer, 2013). This order of cyanobacteria occurs in coprolites from the Permian and Triassic (Northwood, 2005; Bajdek et al., 2016).

4.1.3. Morphotype M3

M3 coprolites are large and thick (64 to 200 mm length and 45 to 85 mm width) cylindrical coprolites, with rounded ends (Fig. 6A–B). The surface is smooth, non-segmented and with rare folds. However, a few specimens have longitudinal striations impressed in the very fine-grained matrix (Fig. 6A). These coprolites are usually straight to buckle-shaped. This morphology occurs in the Permian and was named as *Eucoprus cylindratus* (Hunt et al., 2012). Small gas vesicles are common, and are observed on the external surface of the coprolites and in their matrix when analyzed under an optical microscope.

A single, oval-shaped structure was found in a thin section of an M3 coprolite. This structure is thin, smooth-shelled and is 65 µm long and 50 µm wide (Fig. 6C), which leads us to classify it as an invertebrate egg. Internally, the egg contains a cell structure similar to an early stage of mitosis (Moravec, 2001). Spherical objects around 1.5 µm in diameter are present, which are interpreted as pseudomorphs after bacteria (Fig. 6D; Pesquero et al., 2014). They are present in groups of up to 10 spheres, some of which have thick walls or double layers with a thin void space between that may be the former location of bacterial cell walls. Dumbbell-shaped phytoliths (Fig. 6E) are very common in the M3 coprolite matrix and represent the only plant remains included on these coprolites.

4.1.4. Morphotype M4

M4 coprolites are elongate, narrow and cylindrical (sausage-like shape), with rounded or slightly tapered ends. They are composed of a fine-grained

matrix, and their size varies from 42 to 135 mm long and 18 to 49 mm wide. The M4 coprolites are usually curved or buckled (Fig. 7A), with folds along the entire specimen.

The M4 and M1 morphotypes have some surface marks that are discussed below. In the SEM analyses, elongated parallel structures with polygonal cells (Fig. 7C–D) are found. These structures are approximately 17 µm in diameter and are very similar to the muscle cells described by Chin et al. (2003; Fig. 2B).

4.1.5. Morphotype M5

M5 comprises short, cylindrical coprolites, with a rough surface, and rounded ends. The fecal matrix is coarse grained, and the size ranges from 27 to 61 mm long and 18 to 25 mm wide. M5 coprolites are rich in plant remains, having more vegetal inclusions than other morphotypes. These are represented mainly by Poacea (75% of the plant fragments characterized by parallel-veined leaves; Fig. 8) with a size up to 15 mm. In SEM analysis, a filament of 18.08 µm composed of 5 cells of up to 3.71 µm long and 2.72 wide is interpreted as possibly cyanobacteria (Fig. 8B). These trichomes are similar in size and shape to those of the order Nostocales (Komárek and Hauer, 2013).

4.2. Description of the furrows on the coprolite surfaces

Several series of parallel furrows occur on the surface of the M1 and M4 coprolites (Fig. 9). These structures can occur in pairs or in sets of up to five to

11 parallel furrows, and in some parts are superimposed on each other. These furrows are very similar in shape to those described by Godfrey and Palmer (2015) on the surface of a single coprolite from the Cretaceous–Paleocene Clapp Creek bone-bed of South Carolina, in the USA. As occurs in the North American material, the Venezuelan coprolite traces are composed of slightly curved to straight primary furrows associated with thinner secondary furrows located between the primary traces (Godfrey and Palmer, 2015). In contrast, the materials described here are smaller than those from the Clapp Creek. All of them have one end terminated in conical impressions, suggesting the same fish-biting origin proposed by Godfrey and Palmer (2015). The traces preserved on the specimen LGP-H562 (an M1 coprolite) are represented by at least five primary furrows, 1 mm apart, the larger one being 3.5 mm in length. These traces are located in the middle part of the feces, once it was broken, probably during the moment in which the furrows were produced. Other traces produced in the specimens LGP-H561 are randomly located and smaller than those of the specimen LGP-H562. Among the same coprolites, the traces vary in depth and shape of the bottom (the deep traces are almost U-shaped in cross-section, while in the shallower traces the bottoms are V-shaped), suggesting different biting pressures, probably by the fish mandibles. The specimen LGP-H572 (morphotype M4) has two separate series of parallel furrows (Fig. 9G). Both series have four traces, 0.9 mm apart and up to 4.4 mm in length. These traces are deeper than those preserved on the M1 coprolites and have U-shaped bottoms in transversal section. Some of the serial furrows are related to hollows on the surface of the coprolite, which may indicate coprophagous behavior of the producer of these traces.

4.3. Bioerosion traces in the coprolites

Small, shallow and rounded (at least seven) borings 1 mm in diameter and 1 mm in depth (Fig. 10) are found in the coprolite LGP-H571 of morphotype M3. The size of these structures varies from 9.5 mm in length and 6.3 mm in width in the larger trace to 3.3 mm in length and 2.3 mm in width in the smaller one. They are flask-shaped traces, formed by a main chamber connected to the exterior by a nearly rounded aperture, whose diameter varies from 1.0 to 1.5 mm. The chambers are subspherical to drop-shaped in longitudinal section and circular in cross-section, with smooth walls. The traces have a neck region with conical shape, which connects the main chamber to the aperture. This neck region has an almost triangular shape in longitudinal section, with smooth and straight walls, and a circular shape in cross-section. All of the borings are filled by calcium carbonate (calcite) and preserved as internal molds of the original traces. All of these traces occur close to each other, in the same area of the coprolite. These features are concordant with the diagnosis of the ichnospecies *Gastrochaenolites orbicularis* Kelly and Bromley, 1984, although the Venezuelan traces seems to have short neck regions in comparison with the type species from the Cretaceous of Belgium.

The other ichnospecies of this ichnogenus, *G. orbicularis*, is produced by the mechanical rasping of pholadid bivalves (Tapanila et al., 2004) in a hard substrate. Kelly and Bromley (1984) considered that the producer of the type material of *G. orbicularis* was the myoidean genus *Jouannetia.* There are several examples of bioturbation of fresh dung by coprophilous arthropods

(Chin and Gill, 1996; Mikulás and Genise, 2003; Milán et al., 2012) and mollusks (Chin et al., 2009), but the morphology of the produced traces is not similar to that described here or even to *Gastrochaenolites* traces. Additionally, there are no records of coprophagous bivalves or of *Gastrochaenolites*-like traces produced by these mollusks (or even another group of animals) in fresh dung. Therefore, due to the similarity between the traces on the Urumaco coprolite LGP-H571 and the boring trace *Gastrochaenolites orbicularis*, and the absence of coprophagous traces with a similar shape, we interpret these traces as having been produced after the complete fossilization of the coprolite. In this hypothesis, the bivalves must have eroded a lithic substrate (the fossilized feces), instead of a fresh dung pellet (Fig. 11).

This scenario implies some kind of reworking and subsequent reburial of the fossils from the Cerro Bejucal locality (Fig. 11). Tapanila et al. (2008) described a complex taphonomical history of the vertebrate bones and coprolites from the Eocene phosphatic conglomerates of Mali. The presence of *Gastrochaenolites* borings in these materials is evidence for the presence of pholadid bivalves (the alleged tracemakers) in this paleoenvironment (Tapanila et al., 2004, 2008). This led the authors to consider that fossiliferous conglomerate was submerged in marine or brackish water, followed by a bivalve colonization of lithified feces and bones and other non-biogenic clasts (Tapanila et al., 2008). Although *Gastrochaenolites* occur in less than 1% of the Malian coprolites, the presence of these boring traces in vertebrate bones reinforces Tapanila's et al. (2008) interpretation.

Since *Gastrochanolites* is a very well-known boring trace that only occurs in hard, well lithified substrates (in contrast to a soft, unconsolidated fecal

substrate), we follow here the taphonomical and environmental explanation proposed by Tapanila et al. (2004, 2008). Even though we described only one coprolite with *Gastrochaenolites* from the Urumaco Formation (LGP-H571), we are confident that these borings indicate a more complex taphonomical history for the beds in which it occurs at the Cerro Bejucal locality. However, we are cautious in extending this allegation to the entire Urumaco Formation. The discovery of more *Gastrochaenolites* traces in coprolites and bones from this and other localities should bring more information to this issue.

5. Discussion

5.1. The producers of the coprolites and the paleoecology of the Urumaco Formation

Coprolites with longitudinal striae are known since the Permian (Northwood, 2005; Hunt et al., 2007; Hunt and Lucas, 2012). However, unlike the Urumaco Formation M1 coprolites, they have a carnivorous origin, tentatively attributed to basal archosauromorphs, such as prolacertids or proterosuchids (Thulborn, 1991; Northwood, 2005). In contrast, the M1 coprolites have a rich assemblage of vegetal inclusions, composed mainly of Poacea tissues. Despite the contrasting fossil record, the extant South American coypu (*Myocastor coypus,* Myocastoridae) also produces striated feces with similar size and morphology (Fig. 12; Chame, 2003). However, other caviomorph rodents, such as the extant dinomyid pacarana (*Dinomys branickii*), produce simple cylindrical feces up to 2 cm long, without striae (Osbahr, 2010). The feeding habit of the coypu is composed mainly of grazing grasses,

especially those associated with freshwater bodies (Borgnia et al., 2000; Colares et al., 2010). A similar pattern is inferred for the feeding habits of the M1 coprolite producers, once a high proportion of Poacea were found inside the fossil feces. Caviomorph rodent fossils are very common in the Miocene Urumaco Formation (Pascual and Gamero, 1969; Mones, 1980; Bondesio and Bocquetin-Villanueva, 1988; Horovitz et al., 2006; Vucetih et al., 2010; Carrillo and Sánchez-Villagra, 2015), and some reached huge proportions (Sánchez-Villagra *et al*., 2003; Geiger et al., 2013). Particularly, the outcrop in which morphotype M1 is more abundant (Coquina Bejucal), dinomyids and other indeterminate rodents were also collected (Tab. 2 and 3). Therefore, due to the presence of a great proportion of Poacea inclusions, the morphological similarity between M1 coprolites and the scat of the extant coypu, and the coincident occurrence of rodent body fossils and M1 dung in the same outcrop, we infer that this morphotype is related to rodents, perhaps to myocastorids.

The M2 coprolites resemble in morphology the scat produced by extant ruminants, such as bovids, cervids, giraffids and antilocaprids (Chame 2003; Kropf et al., 2007). These coprolites are rounded to small cylindrical pellets usually pointed at one end and concave at the other extremity. However, terrestrial Cetartiodactyla (such as cervids, camelids and tayassuids) only colonized South America after the early formation of the Panama isthmus, during the Pliocene (O'Dea et al., 2016). Other groups of herbivores, such as the xenarthrans produce coprolites with different morphologies and size (large and cylindrical) (Chame, 2003; Kropf et al., 2007; Hunt et al., 2012a; Hunt et al., 2012b; Hunt and Lucas, 2012). Other herbivores that lived in the Miocene of Venezuela were toxodontid notoungulates and sirenians. Recent sirenian feces

are very different (see discussion of M5 coprolites below). Studies of the feeding ecology of Toxodontidae show that they fed on a mixture of poaceans and eudicotyledoneans (França et al., 2015), like that observed in the M2 coprolites. Thus, we conclude that the animal source of the M2 coprolites was likely toxodontids.

The morphotypes M3 and M4 are characteristic of carnivores, due to the lack of vegetal remains on their matrix and the cylindrical morphology. Milàn (2012) observed and compared scats of 10 species of extant alligatorids, crocodilids and gavialids and concluded that these dungs are very similar in morphology and inclusion type, being basically elongate, cylindrical to tapering, and with rounded ends (Milàn, 2012). Bone and scale remains are completely absent in crocodilian scat. However, hair and feathers were well-preserved (Milàn, 2012). Phytoliths are resistant to the acid attack of the digestive system and were probably ingested with water. Fossil crocodilians are common in the studied outcrops, being represented by alligatorids and gavialids (Scheyer et al., 2013; Scheyer and Delfino, 2016). Therefore, based on the coincident occurrence of these reptiles in the Urumaco Formation and on the morphological and fecal content similarity between the M3 coprolites and recent crocodile scat, there is a strong indication that M3 coprolites could have a crocodilian origin.

Different from the M3 scats, the M4 coprolites are cylindrical and present muscle cells preserved inside the matrix. The sausage-like morphology is similar to various coprolites attributed to Neogene carnivorous mammals (Verde and Ubilla, 2002; Chame, 2003; Carrión et al., 2005; Fugassa et al., 2006; Bravo-Cuevas et al., 2017). However, according to Chame (2003), extant

carnivore scats do not allow diagnosis based only on their size and shape. The order Carnivora is not recorded in the Urumaco Formation, but carnivorous trophic levels are represented by marine and freshwater fishes (Lundberg et al., 1988; Aguilera and Aguilera, 2003, 2004a, 2004b, 2004c; Lundberg and Aguilera, 2003; Aguilera et al., 2008; Aguilera and Marceniuk, 2012; Carrillo-Briceño et al., 2015), crocodilians (Scheyer et al., 2013; Scheyer and Delfino, 2016), turtles (Sánchez-Villagra and Scheyer, 2010; Carrillo-Briceño and Sánchez-Villagra, 2016), snakes (Head et al., 2006) and birds (Walsh and Sánchez, 2008). However, the morphology, content and size does not eliminate a crocodile or even a mammal origin.

Morphotype M5 coprolites were produced by herbivorous animals, as indicated by the presence of Poacea (75%) and Eudicotyledoneae (25%) fragments. The morphology and size of this coprolite resembles those produced by extant manatees (Sirenia, Trichechidae, *Trichechus* spp.*;* Dr. Ioni G. Colares, personal communication, August 18, 2016) and dugongs (Sirenia, Dugongidae, *Dugong dugon*; Dr. Samantha Tol, personal communication, January 18, 2017). Extant manatees have an almost strict herbivorous diet, feeding on all available aquatic and semi-aquatic vegetal species. Among the species that composed the alimentary items of the freshwater and marine manatees, the Poacea are the most common, but other aquatic plants (including seeds), algae, zooplankton (such protozoans, rotifers, cladocerans and copepods) and macroinvertebrates (such crustaceans, mollusks, arachinids and tunicates) were observed in their floating scats or stomach contents (Colares and Colares, 2002; Borges et al., 2008; Castelblanco-Martínez et al., 2009; Guterres-Pazin et al., 2012; Ogogo et al., 2013; and references within).

The extant dugongs feed mainly on Poacea (seagrasses) and occasionally on soft-bodied invertebrates (ascidians, holothurians and hydrozoans; Best, 1981; Preen, 1995; Tol et al., 2016). Being so, the most probable M5 producers were sirenians.

Extant manatees are hindgut-fermenting herbivores with a low metabolic rate, and they are not able to survive in water with temperature lower than 20ºC (Scholander and Irving, 1941, Larkin et al., 2007). Despite this, opportunistic carnivorous behavior has been recorded (Courbis and Worthy, 2003). The extant species of manatees and dugongs occur in tropical waters with large sea grass beds, being able to travel long distances in order to feed (Larkin et al., 2007). In the past, however, dugongs occurred in a very broad territory, including the cold waters of the Bering Sea, inhabited by the Holocene extinct Steller's sea cow (*Hydrodamalis gigas*) (Berta et al, 2006). As indicated by the morphology of the snout and the lack of teeth, some extinct dugongids, such as *Dusisiren*, may have fed on kelp and seaweed (Phaeophyceae, Laminareales) in the water column, rather than the bottom feeding strategy of the extant *Dugong* (Domning and Furusawa, 1995). Dugongids are represented in the Urumaco Formation by the dugongine *Nanosiren sanchezi* and fragmentary bone remains attributed to cf. *Metaxytherium* (Domning and Aguilera, 2008). Here, we presented five morphotypes of coprolite, one of them attributed to sirenians. Despite the recent geographic range of the Trichechidae, manatees were not recovered in the Urumaco Formation, supporting the reasonable attribution of the M5 coprolites to dugongids. As described above, the M5 coprolites contain large amounts of Poacea undigested remains.

Five coprolite morphotypes were recognized in the Urumaco Formation, and the recognition of their producers, as well the presence of distinct associated traces (coprophagy and boring traces) allowed us to access some information about the Late Miocene Urumaco paleoenvironments that were not available before. The presence of a high percentage of Poacea tissues included in morphotypes M1, M2 and M5 indicates that this group of flowering plants was the main food resource available to terrestrial (rodents and notoungulates, respectively the M1 and M2 producers) and fully aquatic (sirenians, M5 producers) mammals. Additionally, the presence of Oscillatorialles and Nostocales trichomes indicates that the producers of the M2 coprolites could have fed on water bodies, where these cyanobacteria occur, or even ingested it when they drank water. Isotopic analyses confirmed that toxodonts could have a mixed-feeder habit of grasses and aquatic plants (França et al., 2015; Viana et al., 2011). Regarding the M1 producers, they were inferred based on the notorious similarity of the morphology of the coprolites with the striated feces produced by the extant coypu (see above). Actually, coypus have an amphibious mode of life, living along rivers, lakes, marshes and swamps of South America (Colares et al., 2010). Therefore, the producers of the M1 and M2 coprolites, here inferred as being rodents and toxodontids, must have had home ranges that included water bodies and even utilized the water bodies and their margins to feed and/or construct their nests.

The presence of fish coprophagy traces on the surface of M1 and M4 coprolites (Fig. 9) is evidence that the animals defecated inside the water body or along its border, and the scat was attacked by dung feeders. Godfrey and Palmer (2015) attributed these traces to gars (*Lepisosteus* sp.) or even

chondrichthyans, which may intentionally (or not) bite the newly produced scat. As pointed out by Godfrey and Palmer (2015), it is not possible to access the location of the scat during the biting, but the hypothesis that the feces were in the water column during the coprophagy best fits the scenario. The fish record of the Urumaco Formation includes at least nine families of bony fishes and 21 taxa of elasmobranchs (Aguilera and Aguilera, 2003, 2004a, 2004b, 2004c; Aguilera and Marceniuk, 2012; Carrillo-Briceño et al., 2015). However, lepisosteid fishes have not been recovered from the Urumaco Formation. On the other hand, several families of toothed fishes occur in the Urumaco paleoenvironment, such as Serrasalmidae (pacus and their relatives), Sciaenidae (drums) and probably Erythrinidae (trahiras) that could have a coprophagous (or at least exploratory) behavior (Aguilera and Aguilera, 2003, 2004; Lundberg et al., 1988; Carrillo-Briceño et al., 2015). Actually, coprophagy habits were observed on the extant serrasalmid *Colossoma macropomum* (Wood et al., 2017), but more data are needed in order to better understand this behavior and the relevant strategies. Thus, the coprolite record of the Urumaco Formation indicates that coprophagy behavior has been present among Neotropical fishes at least since the Miocene.

Parasite eggs are the most common evidence of parasitic interaction with vertebrates (Fugassa et al., 2006; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013; Wood et al., 2013; Da Silva et al., 2014; Hugot et al., 2014; Zatoń and Rakociński, 2014; Bajdek et al., 2016). Helminth infestation on the gastrointestinal tract is common in crocodiles (Moravec, 2001; Batista et al., 2012). The egg found in the M3 coprolite is similar in size and morphology to a nematode egg (see examples in Moravec, 2001).

5.2. Coprolite fossilization

The coprolites were rapidly buried in mudstones/siltstones (Table 1), under anaerobic conditions resulting in little decomposition and the good preservation of undigested residues inside the fossilized scats. These facts are demonstrated by the large number of herbivorous coprolites, rare in the geological record (Chin, 2002; Chin et al. 2003, Northwood, 2005; Chin, 2007; Dentzien-Dias et al., 2012; Bajdek et al., 2016; Niedźwiedzki et al., 2016), since unburied scats can be decomposed by microbes and destroyed by coprophagous insects, trampling or transport.

Carnivorous and herbivorous coprolites have rounded structures that were interpreted as bacterial remains (morphotypes M1 and M3). Two different cyanobacteria filaments were found in the morphotypes M2 and M5, both herbivorous coprolites, and probably produced inside water. According to Newman et al. (2016), elevated concentrations of seawater silica and the delivery of suspended clays promote microbial preservation in a few days. Even though the chemical composition of the Urumaco coprolites and microbial material preserved therein are phosphatic, the same composition indicates the microbial remains were rapidly coated by calcium phosphate. The calcium phosphate of carnivore coprolites is acquired from ingested bones, while the herbivorous can come from ground water that sets up conditions suitable for mineralization by bacterial mediated or inorganic processes (Hollocher and Hollocher, 2012). Being so, the microenvironment formed inside the coprolites

enhanced the preservation of such delicate structures and indicates a fast burial (Hollocher and Hollocher, 2012).

All the coprolites, except the one with *Gastrochaenolites orbicularis,* do not have any sign of transport, and are therefore considered autochthonous. Regarding the presence of the boring trace *Gastrochaenolites orbicularis* on a single specimen (Fig. 10), it is here inferred as being produced in a lithic substrate, the already fossilized coprolite. This fact implies that the feces produced by the Urumaco Miocene fauna were buried and fossilized and, after the complete lithification of the fecal material, some of them were reworked and exhumed, exposing them to boring bivalves (Fig. 11). This scenario is analogous to that proposed by Tapanila et al. (2004, 2008) for the Eocene phosphatic conglomerates from Mali based on the same evidence. As a result of this process, it is inferred that there is some time-averaging of the remains found in the Cerro Bejucal outcrop. Unfortunately, it is not possible to estimate this time-averaging only with this available data, nor to extend it to other outcrops of the Urumaco Formation.

Regarding the producer of the LGP-H571 borings, we assume that myoid bivalves were the most suitable tracemakers, based on the information presented by Kelly and Bromley (1984) and Tapanila et al. (2004) and on the actualistic data provided by Donovan (2013).

6. Conclusions

The coprolite diversity of the Urumaco Formation, with five distinctive morphotypes, and probably different producers, lead us to affirm that the

ichnological material enriches the knowledge of the Miocene of South America. We conclude that three morphotypes (M1, M2 and M5) were produced by herbivores: the M1 was produced most likely by a rodent similar to the South American coypus; M2 by a large ruminant, probably a toxodontid; and M5 by a sirenian. The morphotypes M3 and M4 were probably produced by carnivores, with M3 related to crocodilians and M4 to indeterminate carnivores. A variety of food remains, such as plant remains and muscle cells, have been preserved in a coprolite from the Urumaco Formation, as well as invertebrate and microorganism remains such as possible parasite eggs, cyanobacteria and bacteria. The different coprolite morphotypes identified on the basis of their morphological features and content show similar chemical composition, suggesting that the producers inhabited the water bodies or lived very close to them. Dominance of herbivorous vertebrate coprolites in the fossil record is rare, and the abundance of these remains, and the association with carnivore coprolites, lead us to believe that Urumaco Formation is rare in the geological record, allowing us to accurately infer the paleoecology of the Late Miocene. Also, the evidence of coprophagy and the presence of boring traces in some specimens indicate that the Urumaco Formation fossil record has an intricate and not completely known taphonomic history.

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Captions

Figure 1. Location and stratigraphy of Urumaco Formation (Urumaco Sequence). A. Generalized stratigraphic section. B. Map of the fossiliferous localities of the Urumaco Formation. Stratigraphic column modified after Quiroz and Jaramillo (2010).

Fig. 2: Coprolites (*in situ*) from the Urumaco Formation. A-B. Tío Gregorio locality (A: AMU-CURS-1006; B: AMU-CURS-1008). C-D. El Mamón locality (AMU-CURS-1000-1004).

Figure 3: Different morphotypes from the Urumaco Formation. Scale bar: 3 cm.

Fig. 4: Morphotype M1 coprolites and inclusions. A: Specimen LGP-H561. B: Specimen AMU-CURS-521-R. C: Specimen LGP-H566 with striae in detail. D: Plant cuticular fragment with longitudinal striation pattern in the specimen LGP-H564. E: Plant remains with vascular tissue in the specimen LGP-H564. F: Possible trilete pollen in the specimen LGP-H564. G: SEM image of oval structures interpreted as bacteria, specimen LGP-H566. Scale bars: A–B: 1 cm; C: 2mm; D: 200 µm; E: 50 µm; G: 2 µm. F is in 40x magnification.

Figure 5. Coprolites M2 and inclusions. A. Specimen LGP-H567. B. Specimen LGP-H568. B–C. Macroscopic plant fragments, specimen LGP-H569. E–F. Plant fragments in thin section, specimen LGP-H569. G–H. Filamentous cyanobacteria in thin section, specimen LGP-H569. I. SEM image of plant fragment, specimen LGP-H569. J. SEM image of a stomatum, specimen LGP-H569. Scale bars: A–B: 2 cm, C-D: 3 mm, E–F: 100 µm, G: 50 µm, H: 20 µm, I: 200 µm, J: 50 µm.

Figure 6. M3 coprolites and inclusions. A. Specimen LGP-H570. B. Specimen AMU-CURS-521c. C. Possible parasite egg in thin section, specimen LGP-H571. D. Thin-walled spheres interpreted as pseudomorphs after microbial cell walls, specimen LGP-H571. E. Dumbbell-shaped phytolith, specimen LGP-H571. Scale bars: A–B: 2 cm, C: 50 µm, D: 5 µm, E: 10 µm.

Figure 7. Morphotype M4 and inclusions (specimen LGP-H572). A. Sausage-like coprolite. B. Furrows interpreted as bite traces. C. Elongated parallel structures interpreted as muscle tissue. D. Polygonal cells interpreted as muscle cells. Scale bars: A: 2 cm, B: 4 mm C: 20 µm, D: 100 µm.

Figure 8: Coprolite M5 with inclusions (specimen LGP-H573). A. General overview of the coprolite; B. Cyanobacteria filament in SEM image. C–F. Plant inclusions. Scale bars: A: 2 cm, B: 5 µm, C–F: 2 mm.

Figure 9. Bite traces on the coprolite surfaces. A: Specimen LGP-H561 (Morphotype M1). B–C: Specimen LGP-H562 (Morphotype M1), in two views. D–E: Details of the specimen LGP-H561. F: Detail of the specimen LGP-H562. G: Detail of the specimen LGP-H572 (Morphotype M4). Scale bars: A: 1 cm, B–E: 5 mm, F–G: 1 cm.

Figure 10. *Gastrocahenolites orbicularis* on the coprolite LGP-H571 (Morphotype M3). A–B: Two views of the same trace, showing the main diagnostic features of the ichnospecies. C: Internal (IM) and external (EM) moulds of *G. orbicularis* still in the coprolite. Scale bars: A–B: 5 mm, C: 1 mm. [For 1 column]

Figure 11: Proposed history to the occurrence of *Gastrochaenolites orbicularis* on the LGP-H571 surface: 1: Defecation; 2: Rapid burial and fossilization; 3:

Reworking of the coprolite (with completely or partially exposition) and production of the traces by boring bivalves; 4: Burial of the perfored coprolite and filling on the traces by the matrix; 5: Exposition and collection.

Figure 12: Striated fecal pellet of the extant South American coypu (*Myocastor coypus,* Myocastoridae) from the Estação Ecológica do Taim (Rio Grande, southern Brazil), with noted similarity to the M1 coprolites. Scale bar: 2cm.

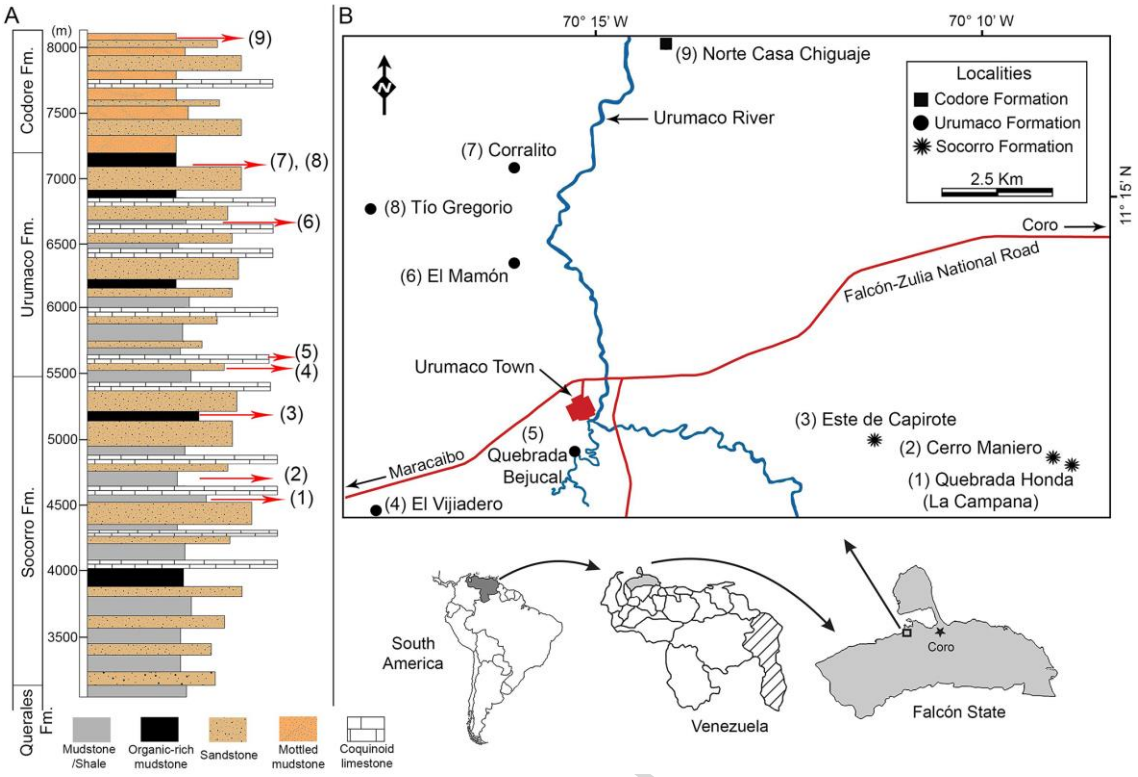


Fig. 1

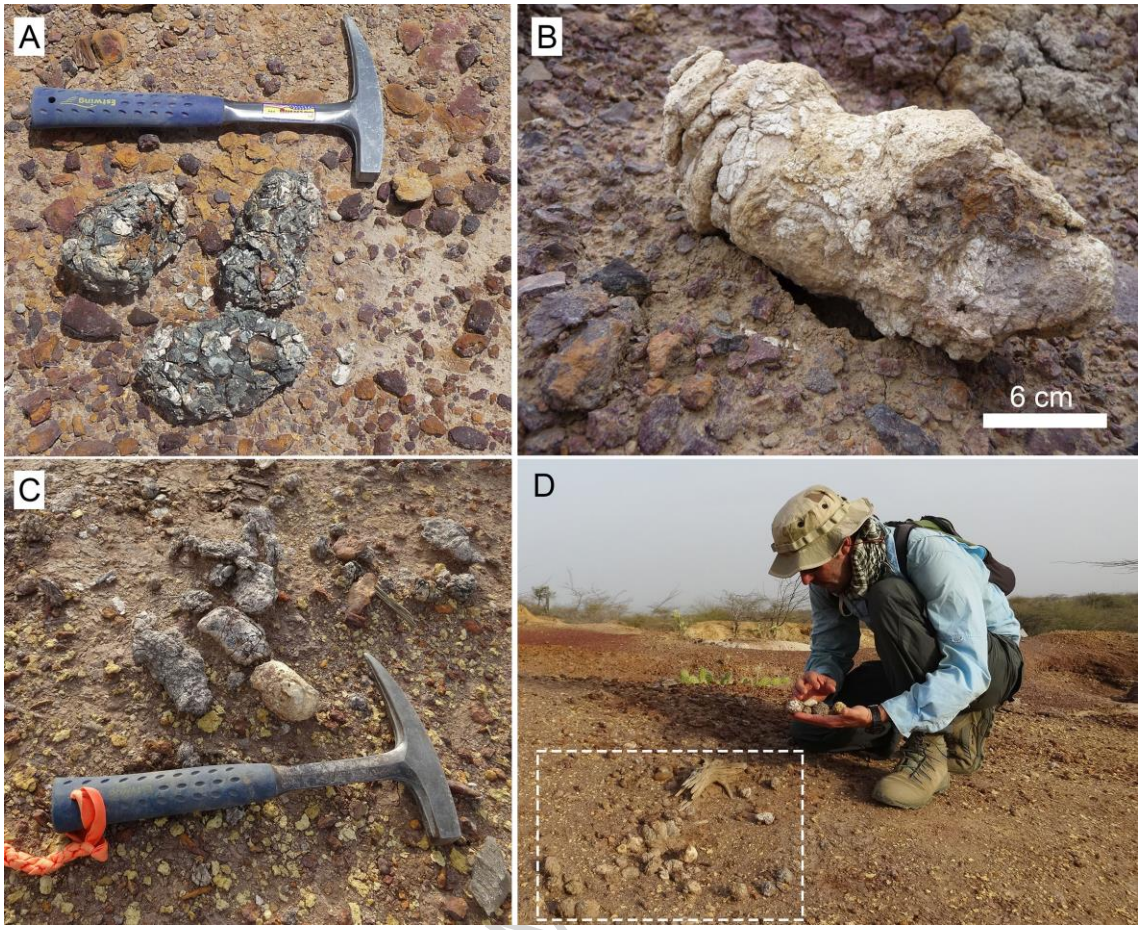


Fig. 2

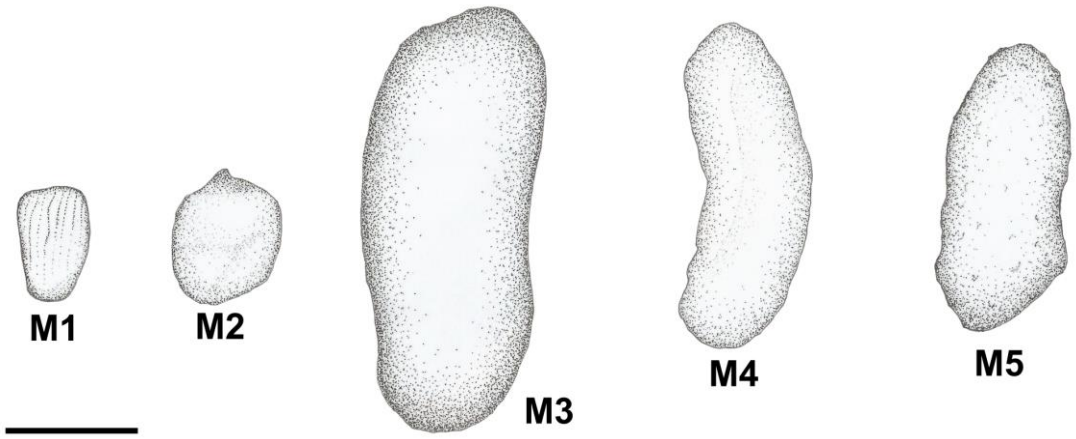
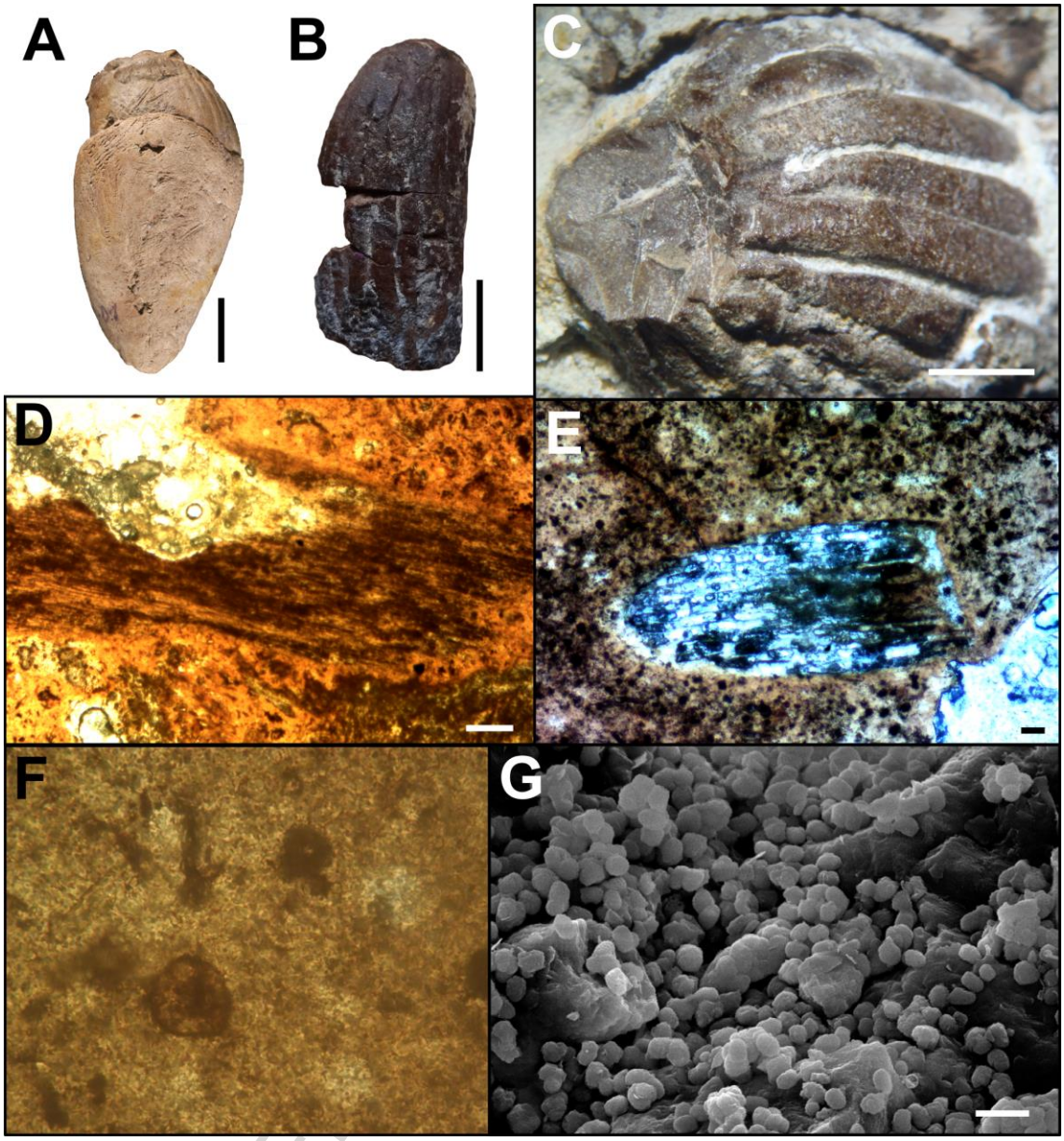


Fig. 3



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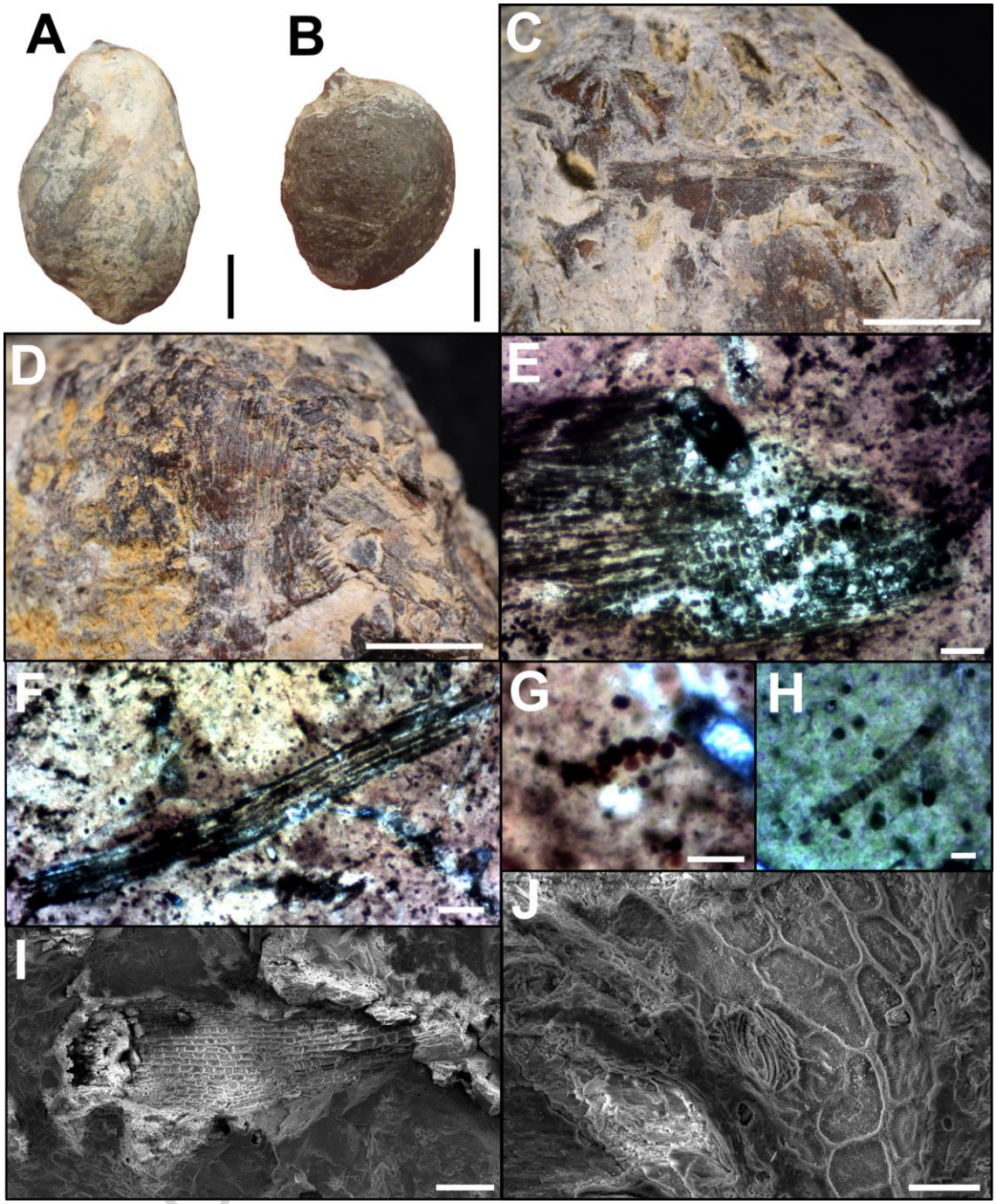


Fig. 5

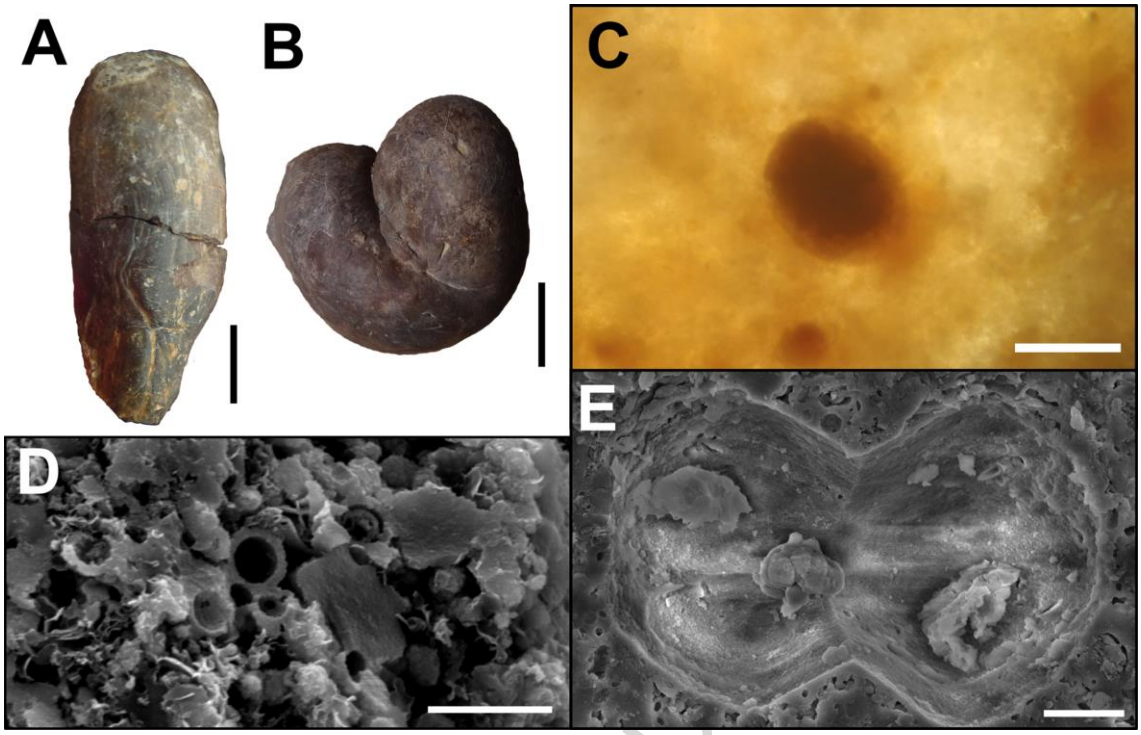


Fig. 6

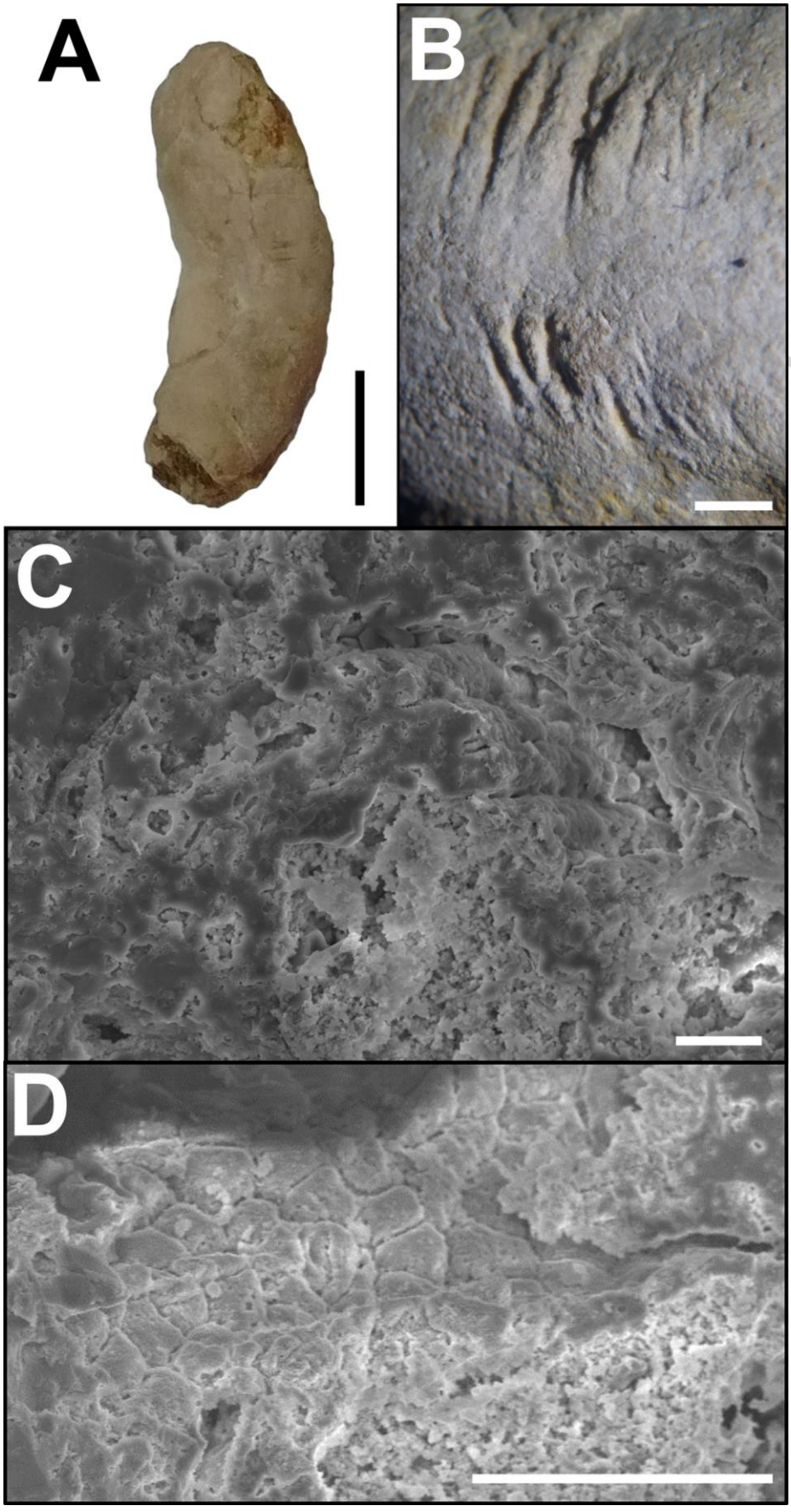


Fig. 7

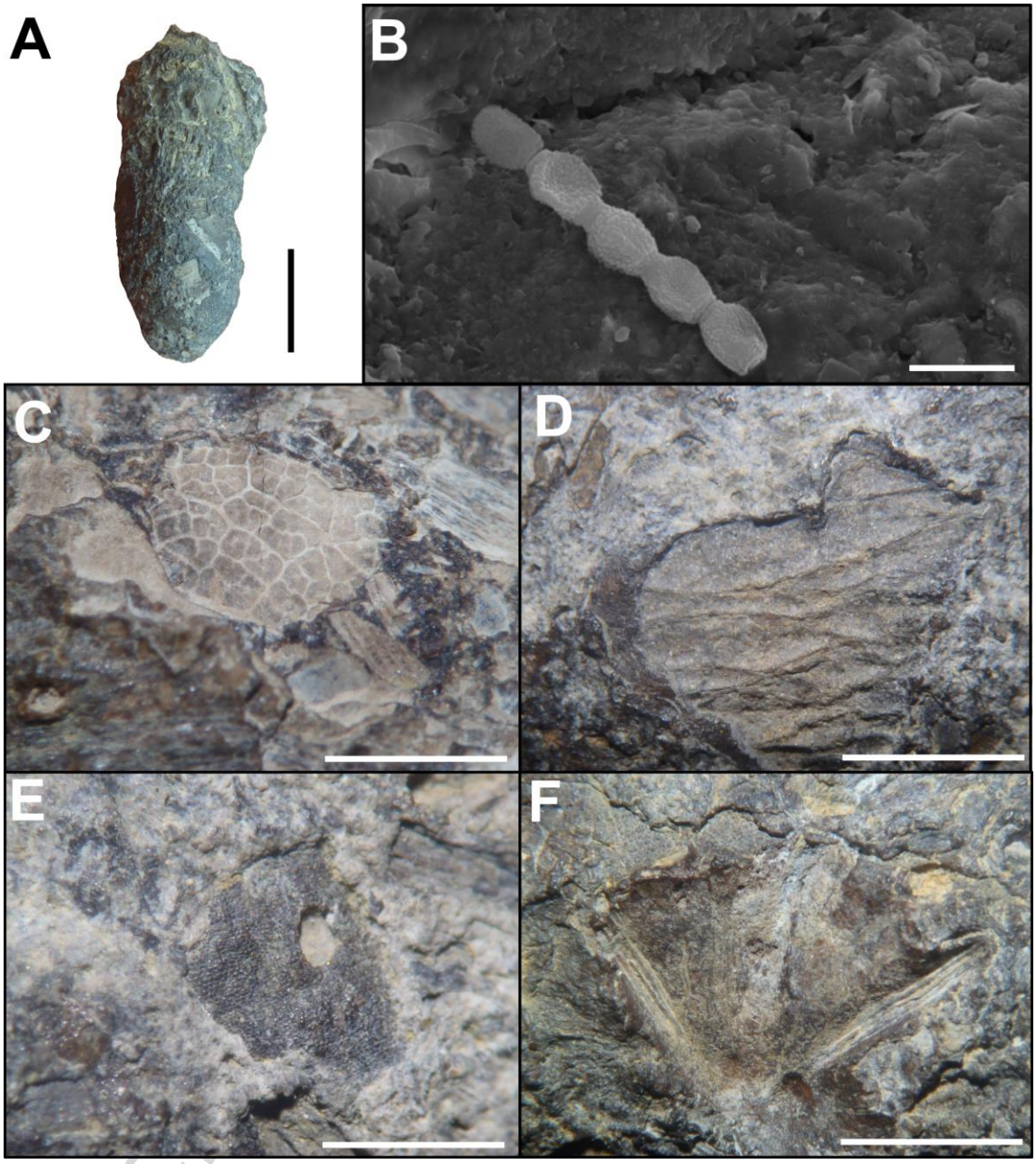


Fig. 8

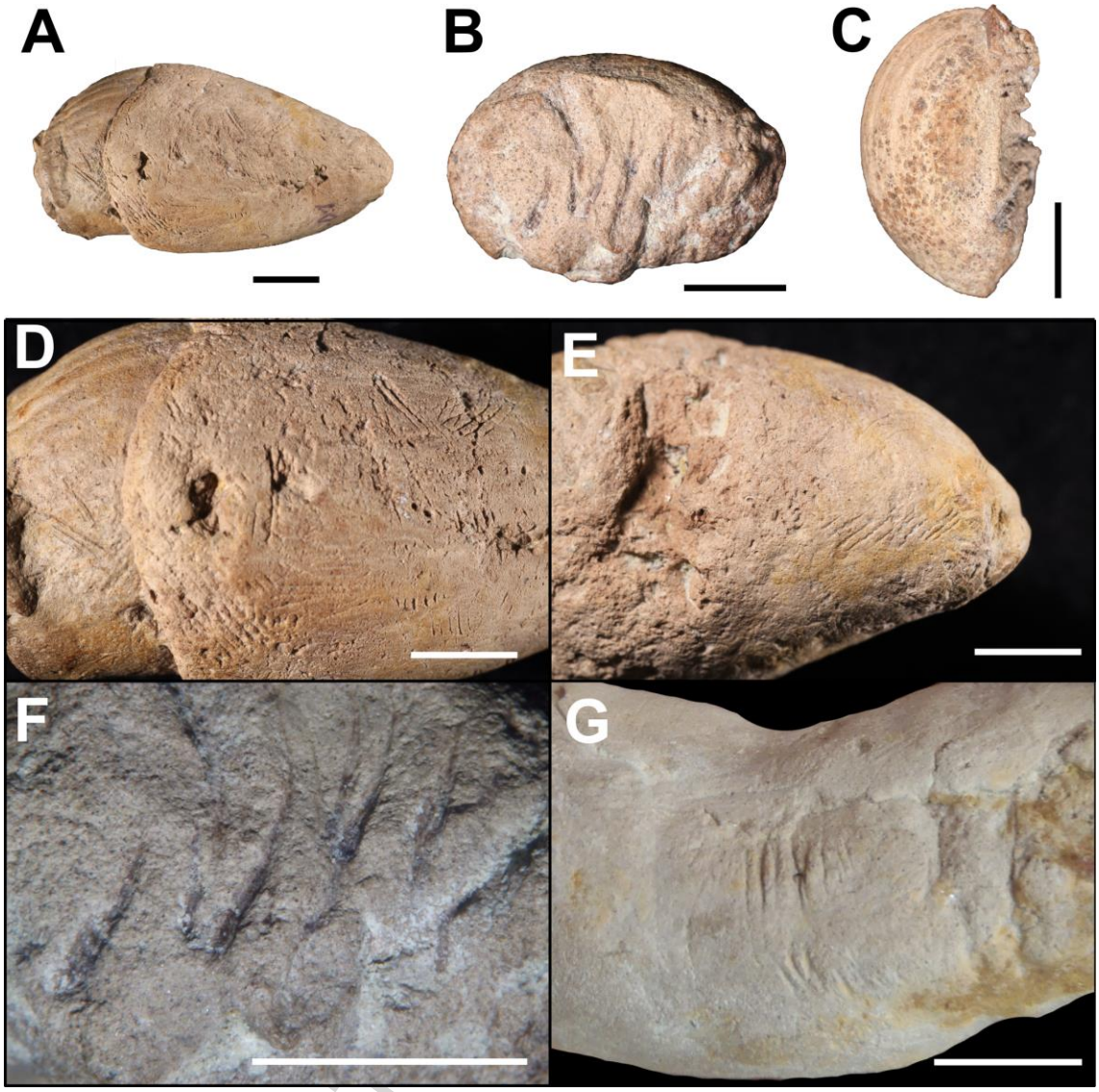


Fig. 9

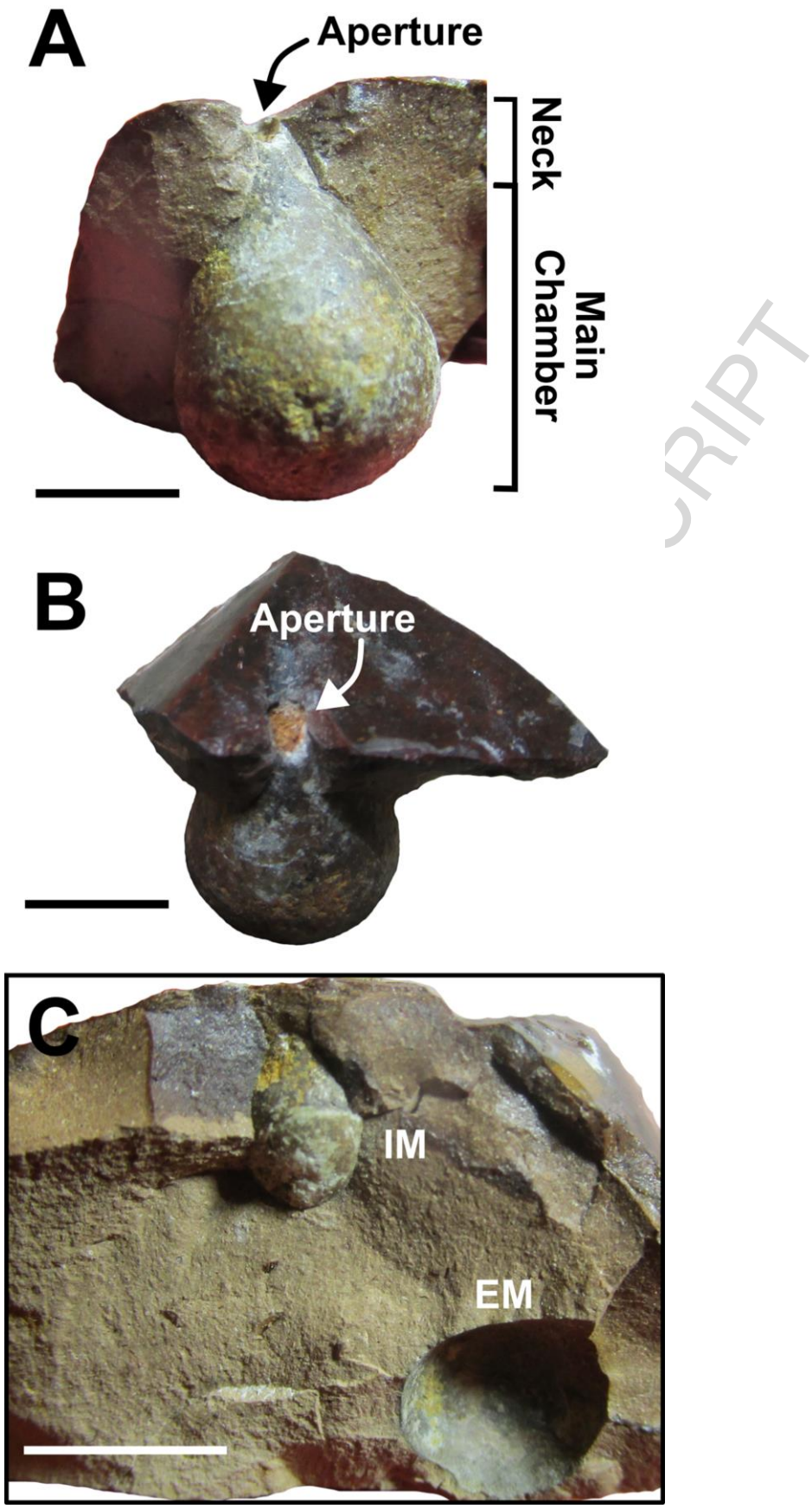


Fig. 10

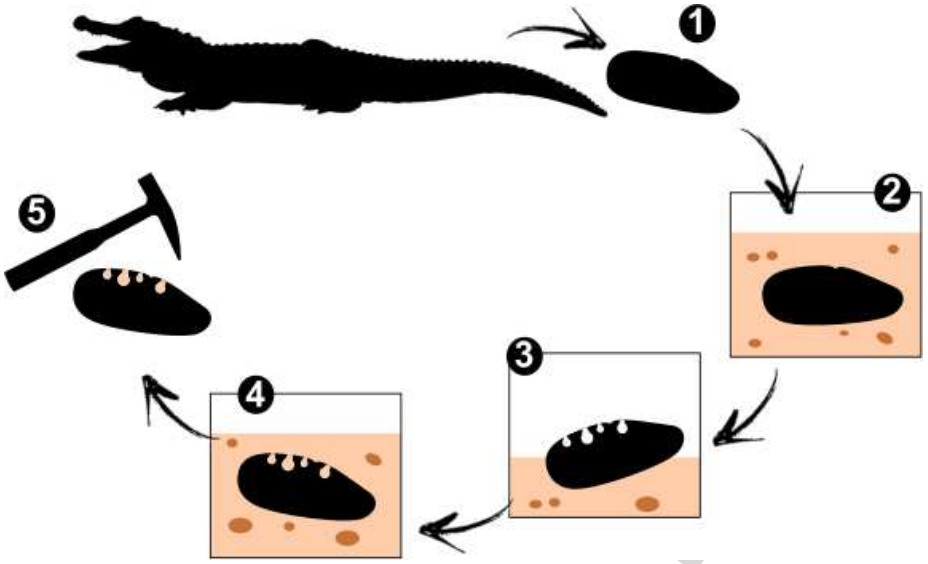


Fig. 11

Fig. 12

Table 1: General information of the lithology and paleoenviroments of the studied coprolite-bearing localities of the Urumaco Formation.

Locality	Formation	Member	Age	Lithology	Paleoenviroment
Tío Gregorio	Urumaco	Upper	Late Miocene	Fine-grained sandstones and organic-rich mudstones	Estuarine/Coastal lagoon, delta plain and floodplain areas
Corralito	Urumaco	Upper	Late Miocene	Interbedding layers of gray-massive mudstones and fine-grained sandstones	Estuarine/Coastal lagoon, delta plain and floodplain areas
El Mamón	Urumaco	Upper	Late Miocene	Interbedding layers of gray-massive mudstones and yellow middle/fine-grained sandstones. Abundant plant remains	Estuarine/Coastal lagoon, delta plain and floodplain areas
Quebrada Bejucal	Urumaco	Lower	Late Miocene	Coquinoid limestone with abundant invertebrate and vertebrate remains	Deposits of a transgression in a interdistributary bay
El Vijiadero (Sur Llano Grande)	Urumaco	Lower	Late Miocene	Interbedding layers of gray-massive mudstones, fine-grained sandstones and organic-rich mudstones	Floodplain areas

Table 2. Coprolite morphotype and fauna from four localities of the Urumaco Formation.

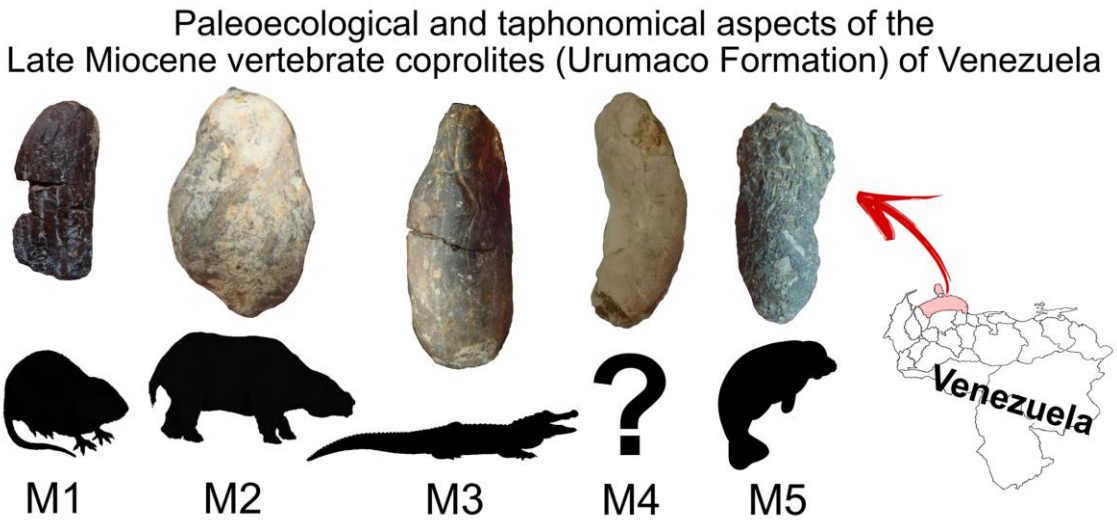
Locality	Morphotypes						Fauna (at family level)
	M1	M2	M3	M4	M5	Indet.	
El Mamón	-	7	7	5	5	26	Chondrichthyes, Osteichthyes Crocodiles (Alligatoridae, Gavialidae), Turtles (Chelidae, Podocnemididae), Snakes (Boidae), Rodents (Dinomyidae), Sirenians (Dugongidae), Cetaceans (Iniidae)
Coquina Bejucal	13	10	7	2	2	4	Chondrichthyes, Osteichthyes, Crocodiles (Alligatoridae), Turtles (Chelidae, Podocnemididae), Snakes (Boidae), Xenarthrans (†Mylodontidae), Rodents (Dinomyidae, Rodentia indet.), Sirenians (Dugongidae)
Corralito	-	-	7	-	-	-	Chondrichthyes, Osteichthyes, Crocodiles (Alligatoridae, Gavialidae), Turtles (Chelidae, Podocnemididae), Snakes (Boidae), Xenarthrans (†Megatheriidae, †Mylodontidae), Litopterns (†Megadolodinae), Notoungulates (†Toxodontidae), Rodents (Dinomyidae), Sirenians (Dugongidae), Cetaceans (Iniidae)
Tío Gregorio	1	3	1	1	-	4	Chondrichthyes, Osteichthyes, Crocodiles (Alligatoridae, Gavialidae), Turtles (Chelidae, Podocnemididae), Snakes (Boidae), Xenarthrans (†Megatheriidae), Notoungulates (†Toxodontidae), Rodents (Dinomyidae), Sirenians (Dugongidae)

El Vijiadero	-	-	1	-	-	-	Crocodiles (Alligatoridae, †Mourasuchus), Turtles (†Stupendemys), Snakes (Boidae), Xenarthrans (†Mylodontidae), Cetaceans (Iniidae)

Table 3. Summary of the coprolites morphotypes and producers.

Morphotype	Morphology	Size		Surface features	Inclusions	Inferred producer
		Maximum	Minimum			
M1	Bullet-shape with longitudinal striations; isolated or in agglomerates	41 mm length/ 38 mm width	17 mm length/ 12 mm width	Borings, bite traces, folds	Plant remains (90% of monocots), trilete pollen, bacterial colonies	Rodents
M2	Rounded to oval with pointed ends	52 mm length/ 31 mm width	23 mm length/ 18 mm width	Folds	Plant remains (80% of monocots), cyanobacteria, hair-like structure	Notoungulata similar to Toxodont
M3	Cylindrical and thick; smooth surface	200 mm length/ 85mm width	64 mm length/ 45mm width	Borings	Gas vesicles, phytoliths, parasite egg, bacterial colonies	Crocodylian
M4	Sausage-like with smooth surface	135 mm length / 49 mm width	42 mm length/ 15 mm width	Borings, bite traces, folds	Muscle cells?	Indeterminate carnivoran
M5	Cylindrical with rough surface and one pointed end	61 mm length/ 25 mm width	27 mm length/ 18 mm width	-	Plant remains (75% of monocots)	Sirenian

Graphical abstract



Highlights

- Coprolites from the Late Miocene Urumaco Formation (Venezuela) are described;
- Five vertebrate coprolite morphotypes, three from herbivorous and two from carnivorous;
- Parasite egg, muscle cells and bacteria occur as inclusions of carnivore coprolites;
- Cyanobacteria, bacterial colonies and plant fragments occur in herbivore coprolites;
- Bite traces and *Gastrochaenolites* are indicative of the taphonomy of the coprolites.